

Evolutionary Ecology of Sympatric *Catocala* Moths (Lepidoptera: Noctuidae)

II. Sampling for Wild Larvae on their Foodplants

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Abstract. Phenologies and foodplant use are documented for wild larvae of 13 species of Nearctic *Catocala* moths whose larvae feed on trees and shrubs in the plant families Juglandaceae, Fagaceae, and Myricaceae. Individual *Catocala* species restricted feeding to one foodplant family, with larvae of 4 species taken only on oaks (*Quercus*), 1 on sweet fern (*Comptonia*), and 8 on hickories (*Carya*) and walnuts (*Juglans*). Taxonomic divisions within Juglandaceae defined further boundaries to foodplant acceptability, with larvae of 2 species found on walnuts, and the other 6 on hickories. All *Carya* feeders preferred shagbark hickory, *Carya ovata*, with 3 of 6 being limited to it. Mature larvae were found on more kinds of foodplants than young larvae of the same species. Larval resting sites shifted from leaves to branches and bark as larvae matured. Different *Catocala* species had differing overall resting sites, with 3 of the 6 *Carya* feeders specializing in hiding under bark. Parasitism was lower in these 3 species compared to species that rest exposed on branches. Periodic competition for food between *Catocala* larvae and gypsy moth (*Lymantria dispar*) larvae is shown to be intense.

Introduction

Although previous workers have generally assumed larval foodplant breadth to be limited among the Nearctic *Catocala* Schrank, little has been published other than *ex ovis* foodplant acceptance of reared larvae. Schweitzer (1982b) has presented some quantitative field data for larvae, documenting that seven Juglandaceae-feeding *Catocala* use shagbark hickory, *Carya ovata* (Mill.) K. Koch (of section §*Eucarya* DC. of *Carya* Nutt.), as a foodplant in southern New England (see also the larval collecting summaries by Rowley, 1909, and Rowley and Berry, 1910). Detailed knowledge of larval foodplant use by the Nearctic Juglandaceae feeders is most desirable, as these taxa have long been known to have synchronous larval and adult phenologies, and 20 or more species occur sympatrically at most locations in eastern North America (e.g., Sargent, 1976, 1977; Miller, 1977).

This paper examines the foodplant-linked biologies of wild larvae of 13 Nearctic *Catocala* species that feed on trees and shrubs in the plant families Juglandaceae, Fagaceae, and Myricaceae. Treated herein are distributions of larvae on different foodplant species, spatial distributions of larvae within individual foodplants, and temporal patterns in

larval abundance. This is the second of three articles examining the evolution of foodplant use in this speciose genus; the other articles cover experimental work on larval foodplant specificity (Gall, 1991a) and female oviposition biology (Gall, 1991b).

Materials and Methods

DESCRIPTION OF STUDY SITES

The primary field study site for larval sampling was West Rock Park, an open-canopied xeric trap rock ridge in New Haven County, Connecticut, USA (see Gall, 1987, 1991a). West Rock is near the northern limit for many elements of more southerly biota and in addition contains the usual fauna and flora of southern New England broadleaf forests. The canopy is dominated by oak, hickory, and ash, with a sparse understory of rosaceous, ericaceous, and other shrubs.

The juglandaceous tree fauna of West Rock is somewhat atypical for southern New England, in that shagbark hickory (*Carya ovata*) is not the overwhelmingly dominant member of this tree genus. Pignut hickory (*C. glabra* [Mill.] Sweet, of section *§Eucarya*) is nearly as abundant as *Carya ovata*, with mockernut hickory (*C. tomentosa* Nutt., of section *§Eucarya*) being less common. Additionally, many of the hickories on the ridgetop are small or medium-sized (5-25 cm dbh), whereas large (>25 cm dbh) hickories are usually encountered in most other New England habitats. On the top of West Rock ridge there are only scattered bitternut hickories (*Carya cordiformis* [Wang.] K. Koch, of section *§Apocarya* DC.) and butternuts (*Juglans cinerea* L.), and virtually no black walnuts (*Juglans nigra* L.). I surveyed other *Juglans* trees (mostly >20 cm dbh) at the base of West Rock, in or near parks in the city of New Haven, and on the Yale campus at the Marsh Botanical Gardens.

There are ten *Quercus* species on West Rock, five each in the white oak (*Lepidobalanus* Endl.) and red oak (*Erythrobalanus* Spach) subgenera, and a non-trivial minority of probable infra-subgeneric hybrids. Seven of these oaks can be found commonly on the ridgetop itself. Among *Quercus* (*Lepidobalanus*) these include: red oak, *Quercus borealis* Michx.; scarlet oak, *Q. coccinea* Muench.; scrub oak, *Q. ilicifolia* Wangenh.; and black oak, *Q. velutina* Lam. Among *Quercus* (*Erythrobalanus*) are: white oak, *Q. alba* L.; chestnut oak, *Q. prinus* L.; and post oak, *Q. stellata* Wangenh. An eighth red oak, dwarf chestnut oak (*Q. prinoides* Willd.), occurs sporadically on the ridge. Swamp white oak (*Q. bicolor* Willd.) and pin oak (*Q. palustris* Muench.) occur only at the base of West Rock.

TECHNIQUES FOR SAMPLING LARVAE

The procedure adopted here is known to lepidopterists as "beating" or "whipping," and variations on the basic theme have long been employed by arthropod workers. First, a close visual inspection of a tree is made for larvae. With trees under 5-10 cm dbh, it is often possible to gently bend the trunk and upper branches down, and thereby inspect the entire canopy. After larvae are removed from reachable branches, a collecting sheet is spread under the tree, and the remaining larvae dislodged from their resting positions by hitting the trunk. For this I used sharp blows with a softball bat, with 1-2 full size bedsheets to catch falling larvae.

While beating might at first seem somewhat inelegant, it is nevertheless a robust and easily implementable quantitative technique. There are a number of

sampling biases to be considered, the four principal ones relevant to juglandaceous foodplants being described here, with others treated in the Results as they pertain to particular questions.

First, by beating one cannot effectively sample the larval faunas of trees much greater than 10-15 cm dbh. This does not greatly affect conclusions in the present study, since the majority of juglandaceous trees on or near West Rock are small and beatable (being young, or occasionally slightly stunted). I did sample larvae from all the large trees which I could both climb and easily reach and beat the principal branches.

Second, the effective sampling radius for any given tree is the width of the collecting sheet. To the extent that this bias is operant for all trees sampled, it would not be expected to alter qualitatively comparisons among foodplant species, assuming tree size class distributions to be largely concordant (cf. Section 1. under Results for Juglandaceae feeders). One expects to sample a somewhat lower percentage of the total fauna of larger trees, since the canopy diameter increases but the collecting surface remains constant.

Third, beating the trunk might not jar a tree enough to dislodge all larvae on branches and leaves. I investigated this possibility often, by first noting the resting locations of *Catocala* and other lepidopteran larvae on hickories (but not removing them), and then beating the trees. The majority (ca. 50-100 percent) of larvae so located usually landed on the collecting sheet, and reinvestigation of the tree showed that the others were no longer at their prior resting sites. These doubtless missed the sheet. Even when a tree was hit lightly, this usually proved sufficient to induce *Catocala* larvae to shift their resting positions and/or move rapidly along a petiole or branch, and moving larvae are quite readily dislodged. When sampling, I would therefore hit a tree several times in rapid succession, wait some 5-15 seconds, and then beat again to dislodge remaining larvae.

Fourth, related to point three, most *Carya ovata* (even some young trees) have long strips of exfoliating bark ("shags") under which larvae can hide and wedge themselves, and it is doubtful that beating dislodges a large proportion of larvae hiding there. Sampling all the shags on a particular tree is impractical, since shags are numerous and often occur to nearly the full height of the tree. Moreover, to search shags thoroughly requires that they be removed or bent substantially, a process injurious to the cambium. Thus, I made a practice of searching under 5-10 shags on suitable trees, after checking the leaves and branches, but before beating.

LARVAL PARAMETERS

For each *Catocala* larva collected in the field, I recorded the sampling date, the species, and foodplant on which it was found. For larvae located by sight, I recorded the resting position using the following categories: terminal leaflet, lateral leaflet, basal leaflet, branch/trunk, or under shags. For most larvae I was also able to record larval instar, which was indexed using a combination of head capsule width, body size, and the instar-specific morphological patterns of larvae of different *Catocala* species. Many wild-collected larvae were subsequently brought back to the lab, where they were reared to maturity to obtain parasitoids, and/or to verify species identity in a few problematic cases.

Wilson (1975) has documented the effects of parasitoids on larval growth in *Catocala antinympha* Hubner, a Myricaceae feeder. Parasitized larvae of all instars had smaller head capsules and smaller body sizes than their unparasitized

counterparts. This can potentially confound determination of instar using these two parameters, and is why my prior rearing experience with *Catocala* — especially knowledge of the instar-specific morphologies of the larvae — was essential to proper analysis. For statistical tests I was conservative, using only two larval age classes to minimize the parasitoid problem: these were mature (ultimate, penultimate, or antepenultimate instar) and young (all earlier instars). I note here that excluding larvae that proved to be parasitized from the total larval sample alters none of the statistics presented in the Results.

TREE PARAMETERS

For each tree, I recorded its species identity, and for most I also determined size and location. I estimated size by dbh, with size classes as follows: small, less than 10 cm; medium, 10-20 cm; or large, >20 cm. The top of West Rock ridge is a narrow plateau, with steep flanking southwestern and northeastern slopes. Two hiking trails run the length of much of the ridge in the vicinity of my study sites, one each on either side of the central plateau. Thus, I defined tree location as either west slope, east slope, or middle slope, with the trails as boundary lines.

All statistical tests of larval patterns used the appropriate observed tree distributions, as necessary, when calculating expected larval frequencies. The same underlying tree distributions were used for both young and mature larval age classes when this factor was tested, since I adjusted sampling effort weekly during each season so that proportions of the three *Carya* sampled daily remained similar ($p > .25$ for each year by G-tests, data pooled into four-day intervals). Other statistical testing followed Gall (1991a).

Table 1. Distributions of juglandaceous foodplants sampled in Connecticut for *Catocala* larvae, as a function of year, location, and tree size.

Foodplant	1980	1981	1982	1983	1984	1985	1986	1987	Total
<i>Carya glabra</i>	17	25	20	25	20	19	38	9	173
<i>Carya ovata</i>	30	63	17	45	40	31	56	11	293
<i>Carya tomentosa</i>	17	16	8	12	7	7	6	2	75
<i>Carya cordiformis</i>	0	0	0	3	0	1	2	2	8
<i>Juglans cinerea</i>	3	3	2	5	3	4	2	3	25
<i>Juglans nigra</i>	15	10	7	11	6	9	8	9	75
Total	82	117	54	101	76	71	112	36	649

Foodplant	Site			Tree size		
	East	Middle	West	Large	Medium	Small
<i>Carya glabra</i>	24	58	52	20	74	66
<i>Carya ovata</i>	29	95	110	28	87	154
<i>Carya tomentosa</i>	2	20	19	6	19	39

Results

JUGLANDACEAE-FEEDING CATOCALA

1. TREE DISTRIBUTIONS

From 1980-1987 I sampled a total of 649 hickories and walnuts for larvae. Of these, 100 were *Juglans*, 541 were *Carya* of section §*Eucarya*, and 8 were *Carya cordiformis* of section §*Apocarya* (Table 1). Many of the same individual trees were sampled in successive years. No individual *Carya* was sampled twice in any given year, though individual *Juglans* often were after 1982. I treat these repeat *Juglans* trees as independent observations, since larvae were removed each occasion (see Section 2. below for statistical discussion).

I sampled more *Carya* from the western slope than either the middle or, especially, the eastern slopes. There were no differences in the frequencies of the three *Carya* sampled as a function of slope and date ($p > .50$ by G-tests, data pooled across all years). For *C. ovata* and *C. glabra* there were highly significant differences in sampling location as a function of year, whereas for *C. tomentosa* there was not ($p < .01$, $p < .01$ and $p > .50$, respectively, by G-tests). This reflects a real biological difference in the microhabitat distribution of *C. tomentosa* (much more common on the west slope than the middle or east slopes) compared to *C. ovata* and *C. glabra*. The significances for *C. ovata* and *C. glabra* can be traced to the fact that I did not collect on the east slope in 1983 and 1987.

I adjusted sampling effort to maintain comparable tree size class distributions among *Carya*, and hence tree size as a function of tree species proved to be the same both within and among years ($p > .10$ in each case by G-tests). Despite these adjustments, the overall frequencies of the three *Carya* foodplants proved marginally heterogeneous as a function of year ($G=23.86$, $df=14$, $p < .05$). This was due to a preponderance of *Carya tomentosa* sampled during the first year of the study ($G=15.64$, $df=12$, $p > .15$, omitting 1980). Tree size also proved marginally heterogeneous among *Carya* ($G=13.496$, $df=6$, $p < .05$), with this being traceable to an excess of medium-sized *Carya glabra* ($G=1.711$, $df=4$, $p > .50$, without it). For each *Carya*, tree size also proved constant as a function of sampling site ($p > .25$ by G-tests for each species).

These heterogeneities in tree sampling have minimal influence on later conclusions about larval foodplant use, with the possible exception of *epione*. In specific: first, regarding the site by year heterogeneity for *C. ovata* and *C. glabra*, few *Catocala* larvae were collected anywhere during 1983 and 1987 (9 percent of the total *Carya* larva sample; 16 percent of *epione*, and 3 percent of all other taxa combined). Second, regarding the 1980 oversampling of *Carya tomentosa*, only *epione* used this foodplant to any significant extent, and sampling in 1980 was late in the season, after most *epione* larvae had pupated.

Table 2. Distributions of wild Connecticut Juglandaceae-feeding *Catocala* larvae: above, by *Catocala* species by year; below, by foodplant species by year.

Species	1980	1981	1982	1983	1984	1985	1986	1987	Total
<i>epione</i>	8	115	3	17	1	5	19	11	179
<i>habilis</i>	4	25	3	1	0	4	0	0	37
<i>judith</i>	1	3	1	0	0	1	0	0	6
<i>neogama</i>	23	8	11	0	0	0	0	7	49
<i>palaeogama</i>	20	42	7	3	3	11	7	3	96
<i>piatrix</i>	0	0	2	1	0	0	1	0	4
<i>residua</i>	11	6	1	1	0	0	0	0	19
<i>retecta</i>	28	35	17	5	6	12	23	1	127
Total	95	234	45	28	10	33	50	22	517

Foodplant	1980	1981	1982	1983	1984	1985	1986	1987	Total
<i>Carya ovata</i>	49	180	23	23	6	28	40	12	361
<i>Carya glabra</i>	17	20	6	3	0	3	7	3	59
<i>Carya tomentosa</i>	5	26	3	1	4	2	2	0	43
<i>Juglans cinerea</i>	3	4	4	0	0	0	0	1	12
<i>Juglans nigra</i>	21	4	9	1	0	0	1	6	42
Total	95	234	45	28	10	33	50	22	517

Table 3. Distributions of wild Connecticut Juglandaceae-feeding *Catocala* larvae, as a function of foodplant species. P = significance level for preference of favored foodplant genus versus all other juglandaceous foods (G-tests or exact multinomial probabilities).

Species	<i>Carya ovata</i>	<i>Carya glabra</i>	<i>Carya tomentosa</i>	<i>Juglans cinerea</i>	<i>Juglans nigra</i>	Total	Favored Foodplant p
<i>epione</i>	128	21	30	0	0	179	<i>Carya</i> <.01
<i>habilis</i>	37	0	0	0	0	37	<i>Carya</i> <.01
<i>judith</i>	6	0	0	0	0	6	<i>Carya</i> .67
<i>palaeogama</i>	68	22	6	0	0	96	<i>Carya</i> <.01
<i>residua</i>	17	2	0	0	0	19	<i>Carya</i> .06
<i>retecta</i>	105	14	7	0	1	127	<i>Carya</i> <.01
<i>neogama</i>	0	0	0	11	38	49	<i>Juglans</i> <.01
<i>piatrix</i>	0	0	0	1	3	4	<i>Juglans</i> <.01
Total	361	59	43	12	42	517	

2. LARVAL PREFERENCES AMONG FOODPLANT GENERA

I collected 517 *Catocala* larvae from the 649 hickories and walnuts (Tables 2-3). A total of 464 were larvae of *epione* Drury, *habilis* Grote, *judith* Strecker, *palaegama* Guenee, *residua* Strecker, and *retracta* Grote; the other 53 were *neogama* Smith and *piatrix* Grote. I did not find larvae of either *obscura* Strecker or *subnata* Grote. All *neogama* and *piatrix* larvae were found on *Juglans*, and 463 of 464 larvae of the remaining six species were on *Carya* (Table 3). The single *Carya*-to-*Juglans* crossover was an antepenultimate *retracta* larva, found on 31 May 1980 on *Juglans nigra* in a New Haven park.

Repeat sampling of *Juglans* trees from 1982 through 1987 biases the foodplant-genus level statistical tests in Table 3. The preferences of *neogama* and *piatrix* for *Juglans* are substantially underestimated by this repeat sampling bias, and, accordingly, the preferences of the other *Catocala* species for *Carya* are slightly overestimated. For *epione*, *habilis*, *palaegama*, and *retracta*, the bias does not affect the biological conclusion — that is, restriction to *Carya* — drawn from the Table 3 statistical tests, since the preferences of these four *Catocala* for *Carya* remain significant if only the 1980 and 1981 larval samples are considered (the years in which no repeat sampling of *Juglans* was done; $p < .01$ for each species by G-tests). However, for *residua*, whose larval samples were small, the test for *Carya* preference is $p = 0.112$ for the 1980 and 1981 seasons. Note that Schweitzer (1982a, p. 258) searched a total of 6 *Juglans* and 10 *Carya* in Connecticut in 1979-1980, using comparable sampling methods, and captured 5 *residua* on *C. ovata*. Inclusion of his additional trees and larvae with the 1980-1981 data from Table 3 gives $p = 0.031$ for preference of *Carya* by *residua*.

3. LARVAL PREFERENCES WITHIN FOODPLANT GENERA

Table 4 shows the foodplant distributions of the six *Carya*-feeding *Catocala* species as a function of larval age. Different species had different preferences among the *Carya* foodplants ($G = 46.07$, $df = 10$, $p < .01$), although all preferred *C. ovata*, and foodplant use broadened in each species as the larvae matured ($G = 7.31$, $df = 2$, $p < .05$). The repeat sampling of *Juglans* effectively precludes a precise analysis of preference among *Juglans* for *neogama* and *piatrix*, but neither of these *Catocala* seemed to discriminate sharply between *J. nigra* and *J. cinerea* ($p > .50$ for each by G-tests, treating the repeats as independent). None of the *Carya* or *Juglans* feeders showed differences in foodplant preference within their foodplant genus as a function of year ($p > .25$ in each case by G-tests, controlling for instar, foodplant, and year).

Young larvae of *epione*, *habilis*, *palaegama*, and *retracta* were all found disproportionately on *C. ovata* ($p < .01$ for each, G-tests). Mature larvae of *habilis*, *residua*, and *retracta* also strongly preferred *C. ovata* ($p < .01$ for each, G-tests). Mature larvae of *epione* remained primarily on *C. ovata*, but not as faithfully ($G = 8.33$, $df = 2$, $p < .05$), and mature larvae of

Table 4. Distributions of wild Connecticut Juglandaceae-feeding *Catocala* larvae, as a function of larval age and foodplant species. Mature larvae are found on more kinds of foodplants than are young larvae of the same *Catocala* species. See text for elaboration and statistical analyses.

Species	Carya Larval Age	<i>Carya ovata</i>	<i>Carya glabra</i>	<i>Carya tomentosa</i>
<i>epione</i>	Young	65	3	16
	Mature	63	18	14
<i>habilis</i>	Young	9	0	0
	Mature	28	0	0
<i>judith</i>	Young	1	0	0
	Mature	5	0	0
<i>palaeogama</i>	Young	23	5	0
	Mature	45	17	6
<i>residua</i>	Young	2	0	0
	Mature	15	2	0
<i>resecta</i>	Young	25	3	1
	Mature	80	11	6

palaeogama were found nearly equally on the three *Carya* species ($G=4.20$, $df=2$, $p>.15$). Young *judith* and *residua* larvae were not analyzed due to small sample sizes, but it seems clear from other field data (Gall, 1991b) and their mature larval profiles that these two *Catocala*, like *habilis*, are restricted to *C. ovata* throughout their larval cycle.

Larvae of *epione* were found overwhelmingly on small *C. ovata* ($G=14.59$, $df=1$, $p<.01$) and small *C. tomentosa* trees ($G=14.01$, $df=1$, $p<.01$; test is large trees against all others). Larvae of the other five *Carya*-feeding *Catocala* were more often found on large *C. ovata* trees ($p<.05$ for each species, similarly), the trend being most pronounced for *habilis*, *judith*, and *residua*.

4. LARVAL PHENOLOGIES

Figure 1 shows larval instar plotted as a function of sampling date, for each of the *Catocala* species collected. For *epione*, *habilis*, *palaeogama*, *residua*, and *resecta*, larval instar increased smoothly as the season progressed ($p<.05$ by ANOVA for each species, for difference in instar as function of date; instar means shown in Table 5). Instars of *neogama* did not increase with sampling date ($p>.25$ by ANOVA), reflecting its greatly staggered egg hatch in comparison to the synchronous egg hatch of the aforementioned five *Carya* feeders. The *Juglans*-feeding *piatrix* has

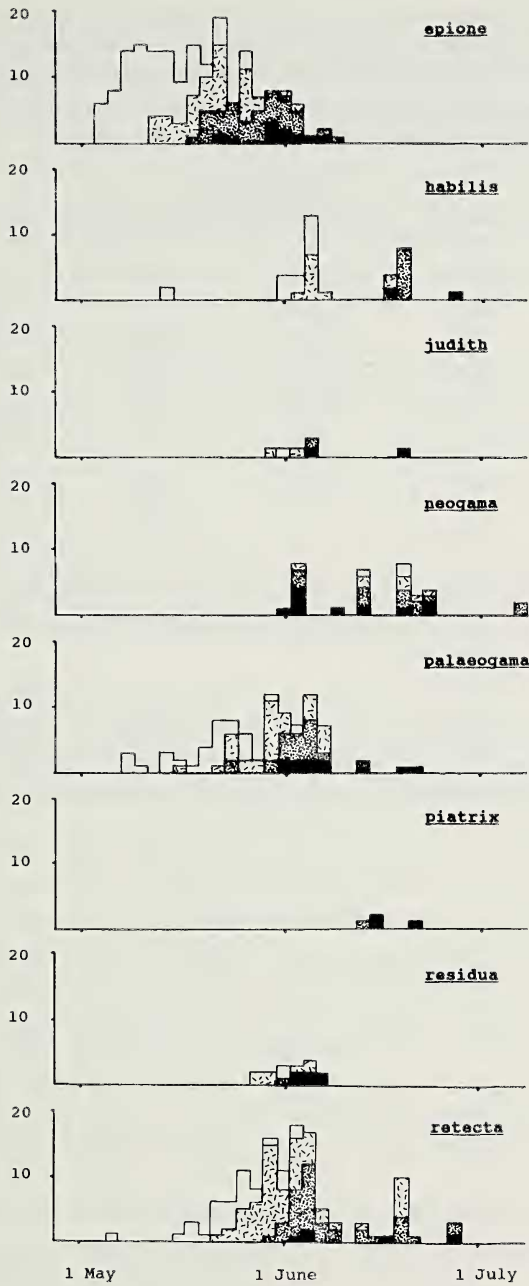


Figure 1. Phenologies of wild Connecticut Juglandaceae-feeding *Catocala* larvae. Black squares = ultimate instars; stippled squares = penultimate instars; hatched squares = antepenultimate instars; white squares = earlier instars. Collection data pooled for 1980 through 1987.

Table 5. Mean collection dates for wild Connecticut Juglandaceae-feeding *Catocala* larvae, by larval instar. Data from 1980 through 1987 pooled, dates begin at 1 May (32 = 1 June, 62 = 1 July). Instar means increase smoothly for *Carya*-feeding species, reflecting synchronous egg hatch; no comparable smooth increase for *Juglans*-feeding species due to asynchronous egg hatch.

Species	Larval Instar				Total
	Younger	Antepenultimate	Penultimate	Ultimate	
<i>epione</i>	10.6	18.3	24.9	26.8	176
<i>habilis</i>	28.6	33.9	47.4	56.0	37
<i>judith</i>	30.0	29.0	34.0	41.0	6
<i>palaeogama</i>	17.6	27.8	31.3	35.9	89
<i>residua</i>	29.0	29.4	29.0	33.7	16
<i>resecta</i>	21.8	30.8	37.1	39.4	126
<i>neogama</i>	45.3	47.0	44.8	38.3	34
<i>piatrix</i>	.	.	42.0	43.3	4

greatly staggered egg hatch, and the *Carya*-feeding *judith* has synchronous egg hatch, but the phenologies of these two *Catocala* were not tested due to small sample sizes.

The 1982 and 1984 larval seasons proved to be significantly later than all other years ($p < .05$ by ANOVA, controlling for instar and *Catocala* species). The 1981 season was earliest, followed quite closely by 1985, 1987, and 1980, with 1983 and 1986 being intermediate; but neither of these trends was statistically significant.

Among the *Carya*-feeding species, larvae of *epione* were found considerably earlier than larvae of the other taxa, and larvae of *habilis* later ($p < .01$ by ANOVA; Mann-Whitney tests used for comparisons involving *judith*). Larvae of *palaeogama* were slightly earlier than those of *resecta* ($p < .05$, similarly), and larvae of the remaining species closely overlapped each other in time ($p > .25$ similarly for each comparison). The timing of egg hatch is the same for these six *Carya*-feeding *Catocala*; hence, the earlier phenology of *epione* can be linked to its larger egg (and more robust first instar larva), and 5 larval instars compared to 6-7 in the other taxa. Larvae of *habilis* simply develop less rapidly than all the others (cf. Gall, 1991a).

For *epione*, *palaeogama*, and *resecta*, whose larvae were found occasionally on foodplants other than *C. ovata*, there were no significant differences in larval collection date as a function of foodplant species ($p > .15$ by ANOVA for each). For *epione*, a tree by instar interaction ($p < .05$ by ANOVA) was due to progressively lower collection date means for mature larvae on *C. ovata* compared to *C. tomentosa* as the season advanced. This probably reflects an accelerated growth rate on *C. ovata* in older *epione* larvae, a pattern also seen in this species' no-choice rearing experiments (Table 4 in Gall, 1991a).

5. LARVAL DENSITIES ON FOODPLANTS

The mean numbers of larvae collected from each tree species are presented in Table 6. Adult *Catocala* were extremely scarce from 1982 through 1984 in southern Connecticut (trap records of myself and D. Schweitzer), and Table 6 reflects this adult scarcity as a 10-fold decline in larval abundance from 1980 through 1984, especially when *epione* is removed (there was a bias against collecting *epione* in 1980, a year in which sampling was disproportionately late in the season). The order of magnitude decline in abundance is highly significant for each foodplant species in Table 6 ($p < .01$ by G-tests, trees split each year into two classes: having no larvae, having one or more larva).

Table 7 shows plots of the number of larvae collected per individual foodplants, by year and *Catocala* species. The variance to mean ratio, an index of contagion, is greater than one for each of these 14 plots, indicating that larvae were not distributed randomly among individual trees. Stated another way, fewer trees than expected had only one larva, and more than expected had no larvae. This makes good biological sense, since the *Carya*-feeding *Catocala* lay varying sized clumps of eggs when ovipositing. The plots also become less contagious as larvae mature ($t=0$, $n=6$, $p < .05$, Wilcoxon test; using those taxa having calculable young and

Table 6. Mean numbers of wild Connecticut Juglandaceae-feeding *Catocala* larvae sampled per tree, as a function of foodplant species. Above, all *Catocala* species included; below, excluding *epione*. Larval densities are always highest on *C. ovata*. Note 10-fold decrease in densities on all foodplants from 1980 through 1984.

	Larvae Per Foodplant Tree							
All <i>Catocala</i> :	1980	1981	1982	1983	1984	1985	1986	1987
<i>Juglans</i>	1.33	0.62	1.44	0.06	0.00	0.00	0.10	0.58
<i>Carya</i>	1.11	2.17	0.71	0.33	0.15	0.58	0.49	0.68
<i>C. glabra</i>	1.00	0.80	0.30	0.12	0.00	0.16	0.18	0.33
<i>C. ovata</i>	1.63	2.86	1.35	0.51	0.15	0.90	0.71	1.09
<i>C. tomentosa</i>	0.29	1.63	0.38	0.08	0.57	0.29	0.33	0.00
Without <i>epione</i> :	1980	1981	1982	1983	1984	1985	1986	1987
<i>Juglans</i>	1.33	0.62	1.44	0.06	0.00	0.00	0.10	0.58
<i>Carya</i>	0.98	1.07	0.64	0.12	0.13	0.49	0.30	0.18
<i>C. glabra</i>	0.94	0.32	0.25	0.08	0.00	0.16	0.05	0.22
<i>C. ovata</i>	1.50	1.57	1.24	0.18	0.13	0.81	0.50	0.18
<i>C. tomentosa</i>	0.12	0.25	0.38	0.00	0.57	0.00	0.00	0.00

Table 7. Numbers of wild Connecticut Juglandaceae-feeding *Catocala* larvae sampled per individual foodplant tree, by year, *Catocala* species, foodplant species, and larval age. Distributions having a plus exclude data from large trees and *Catocala epione*. Variance to mean ratios for all distributions are greater than 1.0, indicating clumping of larvae on foodplants; asterisks show significant clumping i.e., departure from Poisson (0.05 level, G-tests or exact multinomial probabilities).

Species	Larval Age	Year	Foodplant	Number of Larvae					Totals Trees Larvae	Larvae/Tree			
				0	1	2	3	4 >4		Mean	Var/ Mean		
<i>epione</i>	young	1981	<i>Carya ovata</i>	13	2	1	0	1	3	20	40	2.00	9.05 *
<i>epione</i>	mature	1981	<i>Carya ovata</i>	17	8	2	1	0	3	31	30	0.97	2.44 *
<i>epione</i>	young	1981	<i>Carya tomentosa</i>	5	1	0	1	0	2	9	14	1.56	3.07 *
<i>epione</i>	mature	1981	<i>Carya tomentosa</i>	2	0	0	2	0	0	4	6	1.50	2.00
<i>epione</i>	young	1983	<i>Carya ovata</i>	11	0	0	1	2	0	14	11	0.79	4.02 *
<i>epione</i>	young	1986	<i>Carya ovata</i>	16	0	0	0	0	1	17	5	0.29	5.01 *
<i>epione</i>	mature	1986	<i>Carya ovata</i>	34	4	0	1	0	0	39	7	0.18	1.72
<i>habilis</i>	young	1981	<i>Carya ovata</i>	34	1	2	0	0	0	37	5	0.14	1.71
<i>habilis</i>	mature	1981	<i>Carya ovata</i>	8	3	2	1	0	0	14	10	0.71	1.39
<i>palaeogama</i>	mature	1980	<i>Carya ovata</i>	21	4	2	0	0	0	27	8	0.30	1.25
<i>palaeogama</i>	young	1981	<i>Carya ovata</i>	28	4	4	1	0	0	37	15	0.41	1.57
<i>palaeogama</i>	mature	1981	<i>Carya ovata</i>	7	4	2	1	0	0	14	11	0.79	1.37
<i>palaeogama</i>	mature	1985	<i>Carya ovata</i>	12	3	2	0	0	0	17	7	0.41	1.23
<i>residua</i>	mature	1980	<i>Carya ovata</i>	22	4	1	0	0	0	27	6	0.22	1.15
<i>retracta</i>	mature	1980	<i>Carya ovata</i>	16	8	1	0	2	0	27	18	0.67	1.85
<i>retracta</i>	young	1981	<i>Carya ovata</i>	31	4	1	0	1	0	37	10	0.27	2.19
<i>retracta</i>	mature	1981	<i>Carya ovata</i>	11	2	0	1	0	0	14	5	0.36	1.99
<i>retracta</i>	mature	1985	<i>Carya ovata</i>	14	1	1	0	0	1	17	8	0.47	3.49
<i>retracta</i>	mature	1986	<i>Carya ovata</i>	26	7	5	1	0	0	39	20	0.51	1.32
all taxa	mixed	1980	<i>Carya glabra</i>	2	1	2	2	0	0	7	11	1.57	1.03
all taxa	mixed	1980	<i>Carya ovata</i>	9	8	6	1	0	2	26	36	1.39	2.20 *
all taxa	mixed	1981	<i>Carya glabra</i>	7	1	3	0	1	0	12	11	0.92	1.88
all taxa	mixed	1981	<i>Carya tomentosa</i>	7	2	0	1	0	2	12	22	1.83	6.93 *
all taxa	mixed	1981	<i>Carya ovata</i>	21	6	4	7	4	9	51	147	2.77	8.34 *
all taxa +	mixed	1981	<i>Carya ovata</i>	29	7	0	6	5	0	47	45	0.96	2.23 *
all taxa	mixed	1985	<i>Carya ovata</i>	16	6	4	2	0	1	29	26	0.90	2.08
all taxa +	mixed	1985	<i>Carya ovata</i>	16	4	3	1	0	1	25	19	0.76	2.55
all taxa	mixed	1986	<i>Carya ovata</i>	35	13	3	3	0	2	56	40	0.72	2.47 *
all taxa +	mixed	1986	<i>Carya ovata</i>	23	10	5	2	0	0	40	26	0.65	1.23

mature larval samples in the same year), although this analysis is heavily controlled by *epione*, whose larvae clump considerably more than those of the other taxa.

Table 7 also gives similar plots of the number of all *Catocala* larvae collected per tree, by year and by foodplant. Again, the variance to mean ratios are all greater than one, and highly significantly so for *C. ovata* and *C. tomentosa*. The clumping is due neither to the undue influence of *epione* nor to overabundance of larvae on large trees, as shown by the remaining high clumping indices when both these factors are removed

("+" plots in Table 5). This remaining clumping might in part be an artifact of pooling larval age classes. However, with plots having mixtures of *Catocala* species, the tree samples cannot be readily partitioned and tested by groups corresponding to young and mature larvae.

6. LARVAL RESTING SITES

Table 8 shows resting locations for the sampled larvae of the *Carya* feeders, and *Catocala antinympha*, as a function of larval age. The larvae of *antinympha* were collected on West Rock on its myricaceous foodplant, sweet fern (*Comptonia peregrina* [L.] Coult.).

Different *Carya* feeders showed markedly divergent preferences for resting locations ($G=109.40$, $df=2$, $p<.01$). Larvae of all species shifted their resting sites from leaves to woody material as they matured ($G=63.30$, $df=4$, $p<.01$), the magnitude of the change varying from species to species, with *resecta* and *epione* larvae changing their habits most strongly. Comparable age-specific shifts in resting behavior were recorded for *Catocala antinympha* on *Comptonia* ($G=20.96$, $df=1$, $p<.01$).

Table 8. Resting sites for wild Connecticut Juglandaceae-feeding *Catocala* larvae, and larvae of *Catocala antinympha* on *Comptonia peregrina*. Terminal leaflets preferred over other leaflets by young larvae; woody sites preferred over leaves by older larvae. Different *Catocala* species have different overall preferences for type of resting site. See text for statistical analysis.

Species	Larval Age	Leaflet Resting Site			Woody Resting Site	
		Basal	Lateral	Terminal	Branches	Shags
<i>epione</i>	young	5	16	23	4	0
	mature	1	3	3	30	1
<i>habilis</i>	young	0	0	2	4	1
	mature	0	0	1	0	11
<i>judith</i>	young	0	0	0	0	1
	mature	0	0	0	0	2
<i>palaeogama</i>	young	0	6	11	1	0
	mature	0	5	14	6	0
<i>residua</i>	young	0	0	0	0	0
	mature	0	0	0	1	5
<i>resecta</i>	young	2	2	4	0	0
	mature	1	2	2	11	4
<i>antinympha</i>	young		16			1
	mature		3			13

Table 9. Parasitism rates among wild Connecticut Juglandaceae-feeding *Catocala*. Collection data pooled across all years. Parasitism is higher for species that rest exposed on branches compared to species that rest under bark.

Species	Preferred Resting Site	Parasitized	Healthy
<i>judith</i>	hidden under shags	0	3
<i>habilis</i>	hidden under shags	0	12
<i>residua</i>	hidden under shags	0	12
<i>epione</i>	exposed on bark/leaf	15	40
<i>palaeogama</i>	exposed on bark/leaf	7	37
<i>resecta</i>	exposed on bark/leaf	11	73

Table 10. Distributions of wild Connecticut larvae of *Catocala amica* and *Catocala lineella*, as a function of their *Quercus* foodplant species. Larvae of *amica* prefer *Lepidobalanus*, larvae of *lineella* prefer *Erythrobalanus* (see text for statistical analysis).

Foodplant	Trees Sampled	<i>Catocala amica</i>	<i>Catocala lineella</i>
<i>Quercus (Erythrobalanus) borealis</i>	27	2	8
<i>Quercus (Erythrobalanus) coccinea</i>	8	0	0
<i>Quercus (Erythrobalanus) ilicifolia</i>	22	2	3
<i>Quercus (Erythrobalanus) velutina</i>	13	0	0
<i>Quercus (Lepidobalanus) alba</i>	20	4	0
<i>Quercus (Lepidobalanus) prinoides</i>	1	0	0
<i>Quercus (Lepidobalanus) prinus</i>	20	2	2
<i>Quercus (Lepidobalanus) stellata</i>	31	3	2

Among *Carya*-feeding larvae collected on woody material, there were differences in utilization of shags versus branches/trunks ($G=46.43$, $df=5$, $p<.01$), with *habilis*, *judith*, and *residua* specializing in hiding under shags. The low numbers of larvae of these three species collected by beating in comparison to *epione*, *palaeogama*, and *resecta* mostly reflects this difference in resting behavior, as well as my tendency not to search exhaustively under shags on *C. ovata* trees.

Larvae resting on leaves showed a strong preference for terminal leaflets ($G=41.95$, $df=2$, $p<.01$). Table 8 underestimates this preference for terminal leaflets, since the availability is 1:2:2 for terminals, laterals, and basals, respectively, on *C. ovata* and *C. glabra* (or greater, as for example in *C. tomentosa*, which regularly has 7-11 leaflets). The differing leaflets of *Carya* present qualitatively different food resources to *Catocala* larvae, and the influence of leaflet position on larval survival and development, and its more general implications for plant-phytophage interactions, have been treated elsewhere (Gall, 1987).

7. LARVAL PARASITIDS

Table 9 gives numbers of parasitized and healthy larvae, for those wild larvae of the *Carya* feeders that were subsequently brought back and reared in the lab. These data are likely to underestimate the actual parasitism rates in the field, since many young larvae were collected before heavy parasitism might be expected (but note, for example, the several tachinid fly species whose minute eggs are laid on leaf surfaces and ingested by phytophagous larvae). The *Catocala* whose larvae rest primarily under shags (*habilis*, *judith*, *residua*) had significantly lower parasitism rates ($G=9.55$, $df=1$, $p<.01$) than those whose larvae rest exposed on branches and trunks (*epione*, *palaeogama*, *retecta*).

RESULTS: QUERCUS-FEEDING CATOCALA

A sample of 142 oaks was also beaten during 1980-1987 (Table 10). All of these oak trees were classified as small or medium in size. A total of 31 *Catocala* larvae were taken from oaks.

All but 3 of the sampled larvae proved to be *amica* Hubner or its sibling *lineella* Grote. Table 10 gives the distributions of *amica* and *lineella* among their *Quercus* foodplants. Considering only those five oak species on which larvae were taken, these two *Catocala* species had the same foodplant use (but only marginally; $G=8.61$, $df=4$, $.10>p>.05$). Pooling by oak subgenus, these two species differed ($G=4.96$, $df=1$, $p<.05$), *amica* being principally on white oaks, *Quercus* (*Lepidobalanus*), and *lineella* on red oaks, *Quercus* (*Erythrobalanus*).

The other 3 larvae beaten from oaks included 2 *micronympha* Guenee and 1 *coccinata* Grote, all taken on *Quercus stellata*. Curiously, no *ilia* Cramer larvae were captured, as the adults are ubiquitous each year in the study sites (adult *micronympha* and *coccinata* are uncommon there). The absence of *ilia* larvae could in part be due to my sampling rather late in its larval season — the mature larvae tend to rest off the foliage and trunks during the day, and hence would be less collectable during daytime beating. Larvae of *ilia* might also prefer larger trees. Elsewhere in North America, larvae of each of *ilia*, *micronympha*, and *coccinata* have been recorded on trees from both *Quercus* subgenera (my unpublished field records).

Discussion

GENERAL TRENDS IN FOODPLANT SPECIFICITY

The larval records demonstrate that foodplant specificity in these 13 Nearctic *Catocala* species is absolute at the foodplant family level — no larvae of Juglandaceae-feeding taxa were taken on *Quercus*, and no larvae of *Quercus*-feeding taxa were taken on juglandaceous plants. Field data on larval foodplant use for *Catocala* that eat other foodplant genera have also been accumulating recently (Schweitzer, 1987; unpublished field data of myself and others). The conclusion emerging from these studies is that the taxonomic boundaries defined by all nine known

Catocala foodplant families are respected in the field by the larvae (these other collection data will be summarized in the forthcoming taxonomic monograph of the North American *Catocala*).

Within single plant families, foodplant specificity is similarly sharp. At the generic level within Juglandaceae, 2 *Catocala* species in southern Connecticut appear restricted to *Juglans* (*neogama*, *piatrix*), and 6 to *Carya* (*epione*, *habilis*, *judith*, *palaeogama*, *residua*, *retracta*). Adult *subnata* occur near the larval field sites, and I consider the absence of *subnata* larvae on *Juglans* and *Carya* section §*Eucarya* in the present work, and its overriding preference for *Carya* section §*Apocarya* in studies of larval foodplant use (Gall, 1991a) and oviposition (Gall, 1991b) to indicate restriction to *Carya* section §*Apocarya*.

Among the few oak-feeding *Catocala* collected, *amica* appears to prefer white oaks, *Quercus* (*Lepidobalanus*), while *lineella* prefers red oaks, *Quercus* (*Erythrobalanus*). However, the foodplant specificity is not nearly so sharp within these two subgenera of *Quercus* as it is between the Juglandaceae genera.

THE INFLUENCE OF LARVAL AGE

Larval age as indexed by instar proved to be a pivotal variable, and analysis of other factors in the absence of age would have led to erroneous conclusions about the foodplant-linked biologies of all the Juglandaceae-feeding *Catocala* species. This is particularly so for the age specific shifts in resting behavior observed for these *Catocala* larvae (Table 8).

Larval foodplant use broadens as larval age increases (Table 4): mature larvae of *epione*, *palaeogama*, and *retracta* all were more common on *C. glabra* than were young larvae of the same species, and for

Table 11. Species identities of wild Connecticut Juglandaceae-feeding *Catocala* larvae taken on *C. ovata*, for trees yielding seven or more larvae. Asterisks indicate tree samples from Schweitzer (1982b), pluses indicate tree samples from Godwin (unpublished data from tree defaunation studies).

Year	Tree Size	Number						
		Larvae	<i>epione</i>	<i>habilis</i>	<i>judith</i>	<i>palaeogama</i>	<i>residua</i>	<i>retracta</i>
1981	small	26	22	2	0	2	0	0
1981	large	20 *	0	8	1	1	0	10
1981	small	19	15	0	0	3	0	1
1981	large	17 *	0	0	0	5	1	11
1980	medium	15 +	5	0	0	9	0	1
1981	small	11	8	0	0	3	0	0
1982	large	10	2	0	0	4	1	3
1981	medium	9	6	0	0	2	0	1
1981	small	8	8	0	0	0	0	0
1981	large	8	0	3	2	0	3	0
1980	large	7	0	1	0	1	1	4
1979	large	7 +	0	6	0	0	1	0

palaeogama and *retracta*, *C. tomentosa* was used essentially only by mature larvae. This broadening in foodplant use with age is primarily a function of larval movement (differential mortality may contribute to a small extent: in principle, inferior field survival of larvae on *C. ovata* compared to *C. glabra* and *C. tomentosa* could broaden foodplant distributions for mature larvae, but this is known not to be the case for the *Carya*-preferring *Catocala* treated here; Gall, 1991a). In this regard, note that my efficiency at sampling trees was poorest when larvae were mature, for two reasons. First, young larvae rest essentially only on the undersides of leaves, on the midribs, where they are quite visible; mature larvae are cryptically patterned, and shift their resting sites to branches and under shags (but note *palaeogama* which stays on leaves), and so are more difficult to locate. Second, closer visual scrutiny of foodplants is critical when searching for younger larvae, since such small larvae are more likely to be blown by breezes far from the collecting sheet when trees are beaten. Thus, the lack of young (and abundance of mature) larvae on *C. glabra* and *C. tomentosa* is not likely to be explainable by collecting bias.

INTERSPECIFIC LARVAL ASSOCIATIONS

Tables 6 and 7 demonstrate that *Catocala* larvae often co-occur on individual trees (and larval densities are certainly higher in general than indicated here). The corollary question is whether the co-occurrences represent larvae of the same or different *Catocala* species. Table 11 lists the identity of *Catocala* larvae taken on individual *C. ovata* trees from which 7 or more larvae were collected. Several trees from Schweitzer (1982b) and unpublished pyrethrin defaunation studies conducted by B. Godwin are included here (larvae determined by me). All but one tree in Table 11 contains a mixture of at least two species, and most trees have three or four. Note also the field reports by Rowley (1909) and Rowley and Berry (1910) detailing the frequent co-occurrence in Missouri of numbers of *angusi* Grote, *epione*, *habilis*, *judith*, *palaeogama*, *residua*, and *vidua* Smith larvae on *C. ovata*.

The percentage of all trees from which I collected more than one larva, on which two or more *Catocala* species were also present, was high for both *C. ovata* (34 of 57) and *C. glabra* (7 of 11). Furthermore, these percentages remained comparable from year to year, despite the great fluctuations observed in larval densities (for *C. ovata*, $G=5.13$, $df=6$, $p>.50$; for *C. glabra*, $G=3.28$, $df=3$, $p>.25$).

Another way to express the association of different *Catocala* species as larvae is to calculate resource overlap indices. Table 12 lists overlap indices for larvae of the *Carya* feeders, on foodplant use and resting site (the MacArthur-Levins index as modified by Lawlor [1980] was used to reflect consumer electivities i.e., forage ratios *sensu* Stanton [1982] are used as Lawlor's alphas). Table 12 also shows the directional change in the overlap indices between young and mature larvae, and these graphs

Table 12. Overlap indices for wild Connecticut Juglandaceae-feeding *Catocala* larvae, as a function of larval age. Above, for foodplant use; below, for resting site. "Difference" is directional change in overlap index as function of age: zero = change of less than 0.10; plus = increase of more than 0.10; minus = decrease of more than 0.10. "Difference" table interpretable biologically as change in association of different *Catocala* species as larval season progresses.

	Overlap on foodplant use						Difference
	Young Larvae		Mature Larvae		Difference		
	<i>epione</i>	<i>judith palaeogama residua</i>	<i>epione</i>	<i>judith palaeogama residua</i>	<i>epione</i>	<i>judith palaeogama residua</i>	
<i>epione</i>	0.72		0.71		0		
<i>habilis</i>	0.72	1.00	0.71	1.00	0	0	
<i>judith</i>	0.70	0.94	0.96	0.77	+	-	
<i>palaeogama</i>	0.72	1.00	0.77	0.98	0	0	0
<i>residua</i>	0.81	0.97	0.91	0.94	+	0	0
<i>retecta</i>		0.98	0.97	0.94	+	0	0
		0.97		0.96			0

	Overlap on resting sites						Difference
	Young Larvae		Mature Larvae		Difference		
	<i>epione</i>	<i>judith palaeogama residua</i>	<i>epione</i>	<i>judith palaeogama residua</i>	<i>epione</i>	<i>judith palaeogama residua</i>	
<i>epione</i>	0.47		0.04		-		
<i>habilis</i>	0.00	0.22	0.00	0.99	0	+	
<i>judith</i>	0.98	0.45	0.21	0.08	-	-	0
<i>palaeogama</i>		0.00	0.23	0.98	.	.	.
<i>residua</i>	0.95	0.36	0.95	0.33	0	0	+
<i>retecta</i>		0.91	0.95	0.54	0	0	-
			0.91	0.54	0	0	-

are therefore interpretable biologically as the change in association of different *Catocala* species on the same foodplant array over time (refer as well to the larval phenologies given in Figure 1). These overlap indices are offered mainly as instructive guides, since they help visualize the principal findings of the larval collection data; no statistical testing is done on the indices, because in most instances they are based on small larval samples.

Note the uniformly high values for foodplant use overlap, in both young and mature larvae. Larvae of *epione* became more associated with larvae of *resecta* and *palaeogama* on foodplants as larvae matured, but the resting sites of *epione* and *palaeogama* diverged sharply at the same time. Larvae of *habilis*, *judith*, and *residua* strongly overlapped with each other in both foodplant use and resting site throughout the season (each specializes on large *C. ovata* trees, and hides under shags).

The larvae biology of *epione* differs substantially from those of the other five *Carya*-feeding species examined here (5 vs 6-7 instars, early vs later season phenology, small vs large tree preference, broad vs restricted foodplant use among *Carya*). It is notable that the other five *Carya* feeders comprise part of a closely knit monophyletic unit in the genus *Catocala*, with *epione* being removed at considerable distance (on the basis of egg, larval, and adult morphological characters). I suspect that eating Juglandaceae has been arrived at convergently by *epione*.

LARVAL COMPETITION FOR RESOURCES

For *Catocala*, there are at least two distinct resources for which the larvae might compete: food, and avoidance of predators and parasitoids. Although some *Catocala* species appear to be reasonable candidates for studying foodplant competition — particularly the *C. ovata* specialists *habilis*, *judith*, *obscura*, and *residua* — no experimental evidence is yet at hand (Sargent, 1982, conducted intra- and interspecific rearings of *neogama* and *resecta* larvae on *Carya ovata*, but those data do not address foodplant competition among *Catocala*, as *neogama* does not feed on *Carya* in the field). Certainly, the higher parasitism rates for *epione*, *palaeogama* and *resecta* (whose larvae rest exposed on bark) compared to *habilis*, *judith*, and *residua* (whose larvae rest concealed under shags) underscores the importance of resting site to possible larval competition for antipredator niche space (Table 9).

Both Sargent (1977, 1982) and Schweitzer (1982a, 1982b) consider *Catocala* not food-limited, with larval numbers being held low relative to leaf availability by unknown factors, probably predators and parasites. This is a reasonable assumption in years of low *Catocala* abundance, and perhaps whenever large trees are being considered, but seems untenable in years of peak larval abundance, and for most (if not all) times on small trees. One factor alone, the disdain of larvae for basal leaflets (Table 8; Gall, 1987), reduces the effective preferred leaf surface area on all hickories by perhaps as much as one fourth or one third.

Table 13. Right forewing lengths (in mm) of wild-collected adult Connecticut *Catocala* specimens, as a function of species, sex, and severity of gypsy moth defoliation during the year of collection. ANOVA table shows that peak years of gypsy moth defoliation produce smaller adult *Catocala*. See text for discussion.

Species	Foodplant	Sex	Level of Gypsy Moth Infestation			
			At Peak		Below Peak	
			N	mean wingspan	N	mean wingspan
<i>amica</i>	<i>Quercus</i>	female	11	19.2	3	20.7
		male	10	19.3	6	20.7
<i>blandula</i>	Rosaceae	female	8	21.9	3	23.7
		male	9	20.1	3	22.0
<i>connubialis</i>	<i>Quercus</i>	female	3	18.7	1	19.0
		male	4	18.3	3	19.7
<i>crataegi</i>	Rosaceae	female	11	20.5	1	21.0
		male	6	19.2	4	19.5
<i>ilia</i>	<i>Quercus</i>	female	16	34.9	5	37.6
		male	11	35.5	7	37.1
<i>judith</i>	<i>Carya</i>	female	8	23.9	2	26.5
		male	8	25.2	5	26.0
<i>palaeogama</i>	<i>Carya</i>	female	7	34.0	3	35.3
		male	6	32.2	5	33.2
<i>residua</i>	<i>Carya</i>	female	6	32.8	3	34.0
		male	4	31.3	8	33.0
<i>retracta</i>	<i>Carya</i>	female	5	32.8	4	33.8
		male	6	31.0	14	33.8
Source	df	SS	MS	F	p	
sex	1	0.025	0.025	6.90	0.009	
gypsy	1	0.104	0.104	28.90	< 0.001	
species	8	9.493	1.187	328.90	< 0.001	
sex*gypsy	1	0.000	0.000	0.01	0.937	
species*sex	8	0.041	0.005	1.43	0.185	
species*gypsy	8	0.011	0.001	0.38	0.931	
species*sex*gypsy	8	0.015	0.002	0.51	0.846	
residual	183	0.660	0.004			

A relevant factor to intra- and interspecific *Catocala* larval interactions is the influence of the gypsy moth (*Lymantria dispar* L.), an introduced pest that periodically defoliates deciduous forests in North America. Gypsy moth larvae defoliated many canopy trees locally at my West Rock study sites throughout 1980 and especially 1981. In 1981, defoliation was essentially complete for all tree species by the first few days of June. Defoliation of *C. tomentosa* occurred well before other *Carya* species, although by early June most of the *C. ovata* had been stripped of 90-100 percent of their leaves (most oaks had been stripped by late May).

In 1981, only *epione* among the Juglandaceae feeders would have been able to pupate in numbers prior to the brunt of the gypsy moth defoliation (but note the earlier defoliation of *C. tomentosa*, which *epione* uses heavily). On 2 June 1981, I collected 31 *Catocala* larvae, representing all six of the West Rock *Carya*-feeders, from 10 *C. ovata* trees from which the foliage was nearly or entirely stripped by gypsy moth larvae. Only 5 of the 31 larvae were in the final instar; with little question, the remaining 26 would either have died from starvation within a few days, or have been forced to pupate at subnormal larval size.

Indeed, wild adult *Catocala* collected at West Rock and North Stamford, Connecticut, during the years of peak gypsy moth abundance were significantly smaller than adults taken in the same areas in years when gypsy moths were scarce (Table 13). This adult size difference is almost certainly the result of forced early larval pupation in response to lack of foliage. Note that the peak years for gypsy moth abundance at both Connecticut sites were also peak years for *Catocala* abundance, and so the observed dwarfing could perhaps in part be due to increased intraspecific competition between *Catocala* larvae. However, dwarfed adults are not associated with peak *Catocala* years in other localities in the United States where the gypsy moth is absent (personal observations in Arkansas and Tennessee). Additionally, collecting of *Catocala* adults at artificial bait sources was extraordinarily successful in the peak gypsy moth years compared to other years, especially at the beginning of the flight period for each *Catocala* species. Again, this likely indicates that adult moths had to bolster their reduced somatic reserves carried over from larval feeding, prior to mating and oviposition (my unpublished field notes and those of D. Schweitzer).

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